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The classification and structure of megafaunal assemblages in the Venezuela Basin, Caribbean Sea

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ABSTRACT

Data from 23 benthic trawls collected from the Venezuela Basin (3411-5062 m water depth) indicate that megafauna are less abundant than in basins of similar depths in the Atlantic and are segregated by sedimentary province. Taxonomic assemblages, in terms of abundance and biomass, from three sites coincide with distinctions of sedimentary characteristics among the pelagic, hemipelagic and turbidite sedimentary provinces. Mollusks, decapods and fishes are most abundant in trawls collected from the pelagic and hemipelagic provinces and anemones and holothurians are most abundant in trawls collected from the turbidite province. Sponges dominate the biomass of fauna in trawls collected in the turbidite and hemipelagic provinces and fishes dominate the biomass of trawls collected in the pelagic province. Several biological and physical aspects of the basin contribute to the segregation of the megafauna into distinct communities. Sponges and anthropogenic debris (coal, coal clinker and tar balls) reaching the sea floor create a habitat that is exploited by sessile suspension feeders requiring a hard substrate. Filter-feeding anemones attached to debris occur in such abundance that it elevates the importance of suspension feeders and depresses species diversity at the turbidite site. Biomass and average size of megafaunal deposit feeders in the basin decrease with decreasing amounts of organic carbon and nitrogen content of the sediment. Distribution and composition of filter-feeding megafaunal biomass in the Venezuela Basin are explained largely by proximity to sources of organic matter. Detrital carbonate may also play a role in controlling distribution and density of megafauna by diluting food resources in the sediments.

1. Introduction

Most surveys of the deep-sea bottom fauna undertaken since the Challenger Expedition have been exploratory in nature and only recent studies have resulted in quantitative estimates of faunal density and biomass. These quantitative data have been used to characterize megabenthic faunal assemblages based on catch rates of major taxa, diversity indices and dominant species (Rowe and Menzies, 1969; Haedrich *et al.*, 1975, 1980; Rex, 1981; Rowe *et al.*, 1982; Carney *et al.*, 1983; Lampitt *et al.*, 1986; Thurston *et al.*, 1994). Distribution of megabenthic faunal assemblages typically corresponds with bathymetric zones, sediment type, temperature, pressure, submarine currents, and surface water

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productivity (Haedrich *et al.*, 1980; Rowe *et al.*, 1982; Hecker, 1990; Thurston *et al.*, 1994). Additional studies have emphasized the importance of differences in food resource availability (Sibuet *et al.*, 1989) and biological interrelationships such as competition, predation and resource partitioning as causes of zonation of deep-sea benthic fauna (Rex, 1977; Carney *et al.*, 1983; Jumars *et al.*, 1990). Increased awareness of biological diversity as a resource has highlighted the importance of measures of diversity in, among other environments, the deep sea (Grassle, 1989).

Very little knowledge about the deep-sea megabenthic community structure is known because researchers visit this realm infrequently and sample with nonstandardized equipment (Jumars and Eckman, 1983). Another obstacle is that many species encountered in deep-sea collections are as yet undescribed in the literature. Despite the paucity of quantitative data for the deep-sea megabenthic community, several paradigms have emerged from data collected at several abyssal sites. According to the prevailing paradigms: abundance and biomass of megafauna decrease with increasing depth or distance from shore, abyssal regions of the deep sea support high (yet variable) megafaunal species richness, abundance of suspension feeders decrease with increasing depth or distance from shore, and most abyssal megafauna exhibit cosmopolitan distributions (Gage and Tyler, 1991).

In 1981 the USNS *BARTLETT* conducted a box coring and trawling study of the Venezuela Basin in the Caribbean Sea during which epifauna and shallow-dwelling infauna were collected to determine the effects of biological processes on deep-sea sedimentary structure. The basin can be divided into three major sedimentary provinces: pelagic carbonate, turbidite, and hemipelagic (Briggs *et al.*, 1985). The quantity and diversity of benthic microfauna (Harvey *et al.*, 1984), meiofauna (Tietjen, 1984; Woods and Tietjen, 1985), and macrofauna (Richardson *et al.*, 1985) were reported for these three sedimentary regimes. Although megafauna from the Venezuela Basin have been reported on in terms of taxonomy (Gore, 1983, 1984, 1985a,b; Anderson *et al.*, 1985; Riemann-Zürneck, 1986), sediment-reworking activities (Young *et al.*, 1985), and standing stock (Richardson and Young, 1987), analysis of the community structure has not been presented. The purpose of this paper is to describe patterns of species composition and diversity in benthic megafaunal assemblages. Only rarely do we obtain a comprehensive list of all megafaunal species and detailed sediment property data from the deep sea, and we exploit this wealth of information to discuss the influence of sediment type on benthic community structure and the relationships of individual size and abundance of the megafauna to food sources in the deep sea.

2. Materials and methods

a. Site descriptions. The three sites selected and depicted in Figure 1 are representative of the three major sedimentary provinces of the Venezuela Basin, Caribbean Sea (Matthews and Holcombe, 1985). The pelagic site, comprised of foraminiferan tests, pteropod shells and coccoliths is located in the western part of the basin on the eastern flank of the Beata

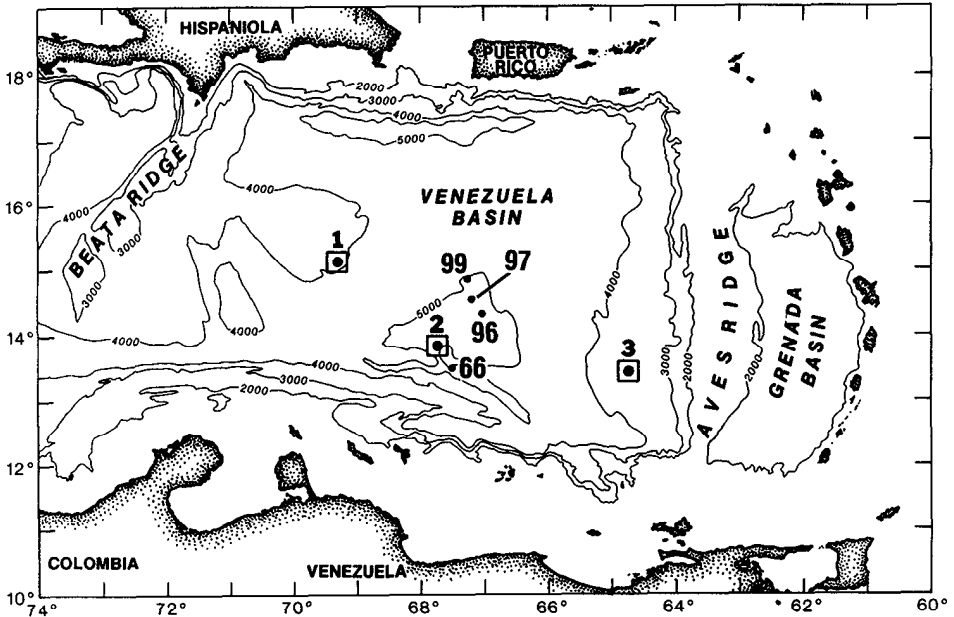


Figure 1. Locations of the three sampled sites in the Venezuela Basin: (1) pelagic province, (2) turbidite province, (3) hemipelagic province. Outlying trawls 66, 96, 97 and 99 are included among the samples from the turbidite province.

Ridge. The turbidite site, characterized by a carbonate-depleted pelagic layer overlying ponded shelf-derived sediments from turbidite flows, is located on the central Venezuela Basin abyssal plain. The hemipelagic site, comprised of pelagic-derived carbonate sediment mixed with terrestrial sediment originating from outflows from the Orinoco and Amazon Rivers, is located in the eastern part of the basin on the western flank of the Aves Ridge. The benthic realm of the Venezuela Basin is considered to be a low energy environment devoid of strong bottom currents (Matthews and Holcombe, 1985; Kinder *et al.*, 1985), and is characterized by numerous and diverse examples of bioturbation (Young *et al.*, 1985). Table 1 displays a summary of the physical characteristics of the three sites

Table 1. Physical characteristics of the three sites in the Venezuela Basin. Values of sediment properties are averages of the top 10 cm of sediment (from Briggs and Richardson, 1984).

Site	Pelagic	Turbidite	Hemipelagic
Depth (m)	3950	5050	3450
Latitude	15°08'N	13°45'N	13°30'N
Longitude	69°16'W	67°45'W	64°45'W
Sediment type	Clayey sand	Clay	Sand-silt-clay
Percent carbonate	66–67	3–6	25–27
Organic C (% dry wt)	0.30	0.70	0.54
Organic N (% dry wt)	0.05	0.13	0.11

Table 2. Trawl station data from the three sites in the Venezuela Basin.

Province	Station	Depth (m)	Area Trawled (m ²)
	No.		
Pelagic	35	3952–4017	9.99×10^4
	36	3952–4044	4.22×10^4
	37	3995–4095	5.77×10^4
	38	3934–4013	6.44×10^4
	39	3993–4064	6.66×10^4
	40	3957–4013	3.77×10^4
Turbidite	58	5044	1.11×10^5
	60	5046	6.22×10^4
	62	5050–5055	1.11×10^5
	63	5046	1.11×10^5
	64	5047	8.88×10^4
	65	5046	1.22×10^5
	66	4944–5062	7.33×10^4
	96	5057	1.18×10^5
	97	5055–5060	1.27×10^5
	99	4956–4997	1.07×10^5
Hemipelagic	87	3481–3517	6.66×10^4
	88	3517–3549	7.77×10^4
	90	3422–3464	7.33×10^4
	91	3459–3507	6.88×10^4
	92	3475–3517	9.55×10^4
	93	3411–3459	8.88×10^4
	94	3427–3475	7.77×10^4

investigated. Data on the grain size, porosity, shear strength and acoustic properties of the basin sediments are presented in Briggs *et al.* (1985).

Renewal of Venezuela Basin bottom water is restricted to warm, saline North Atlantic water due to sill depths of 1815 m or less (Kinder *et al.*, 1985). Consequently, bottom temperature and salinity are relatively constant at 3.83 to 3.86°C and 34.976 to 34.986‰, respectively (Sturges, 1965). Dissolved oxygen concentration of the bottom water is a uniform 5.1 ml L⁻¹ (Anon., 1986). Surface currents transport terrigenous clay particles northward and westward from the eastern coast of South America, through the Lesser Antilles and into the Venezuela Basin. Both sedimentation rate (Cole *et al.*, 1985) and surface primary productivity (Couper, 1983) exhibit northwestward directed decreases across the basin.

b. Field collection and analyses. The faunal data presented here were collected in a total of 23 hauls during a cruise aboard the USNS *BARTLETT* from 14 October to 8 December 1981 (Table 2). The nets were 41-ft (12.5 m) semi-balloon shrimp trawls fabricated by the Marinovich Trawl Company of 1½-in (3.7 cm) stretch mesh with a ½-in (1.27 cm) stretch mesh heavy knotted liner in the cod-end. The nets were deployed as described in Haedrich

Table 3. Catch rates (numbers and wet weights in grams) of major taxa as a function of sedimentary province. Catch rates for "Megafauna" include minor taxa not listed.

Group	Sedimentary Province		
	Pelagic	Turbidite	Hemipelagic
Mean weight (g h ⁻¹)			
Sponges	223.30	1113.00	2064.40
Coelenterates	5.61	7.84	51.62
Mollusks	6.56	2.52	14.25
Decapods	88.83	25.40	87.01
Echinoderms			
Asteroids	51.53	19.66	69.22
Ophiuroids	0.12	0.01	2.36
Holothuroids	100.91	470.39	422.13
Fishes	586.05	283.00	474.66
Megafauna	1079.90	1922.40	3187.20
Mean number h ⁻¹			
Coelenterates	14.79	20.12	9.76
Mollusks	8.60	0.43	14.38
Decapods	5.93	2.25	5.77
Echinoderms			
Asteroids	6.84	1.73	3.22
Ophiuroids	0.13	0.10	3.82
Holothuroids	13.55	8.63	24.31
Fishes	18.41	1.32	7.62
Megafauna	77.64	35.53	69.84

et al. (1980), except for the addition of a time-depth recorder which was attached to the head-rope to record bottom fishing time. We define megafauna as all species large enough to be retained by the stretch mesh liner in the cod-end of the trawl. Mesopelagic fishes and invertebrates were excluded from analyses. Abundances of sponges were not tabulated in terms of number but only in terms of biomass (Table 3). No corrections were made to account for the large contribution of the siliceous skeleton to the sponge wet weight. Inclusion of the skeletal component may be justified by the fact that the organisms must invest energy to produce the spicules as well as the spongin fibers and thus, *in-toto* wet weight represents biomass due to secondary production.

The megafauna were counted, weighed, measured, identified to species and then quantified as numbers of individuals and biomass captured per hour of bottom trawl time. Area swept by the trawls in Table 2 was determined using the estimate of 2.22×10^4 m² swept h⁻¹ given by Percy *et al.* (1982). The hauls from individual sites were clustered together except for stations 66, 96, 97, and 99, which were 42 km southeast, 80 km northeast, 97 km northeast, and 122 km northeast of the turbidite site, respectively (Fig. 1). Inclusion of these four stations with the remaining stations of the turbidite site was justified initially by their common depth range and location within the broad abyssal plain of the basin. These four stations were ultimately grouped with the turbidite stations based on

statistical classification of faunal distribution. We compared our results to abyssal transects south of New England (Haedrich *et al.*, 1980) as well as two other abyssal sites from the Atlantic (Thurston *et al.*, 1994). Trawl catches were quantified as grams and number per m² by using the areal estimate of Pearcy *et al.* (1982) for comparison with the data of Thurston *et al.* (1994).

We determined the patterns of faunal distribution and the community structure of megabenthic assemblages using classification techniques and measures of species dominance and diversity. The Bray-Curtis dissimilarity coefficient was chosen to classify both species and site groups because of its sensitivity to dominance in sample (trawl) classification and abundance in species classification (Richardson, 1976; Boesch, 1977). Site classification was based on square root transformed species density and cube root transformed species biomass values. Transforms increase the importance of rarer species in the classification analysis without unduly reducing the importance of dominant species. Both values of species density and biomass used for species classification were log transformed. All transformed data were standardized (i.e., proportional values of transformed biomass and density over all trawls for species classification and over all species values for each trawl for site classification). Standardization allows species classification to be based on patterns of relative abundance rather than on overall abundance (i.e., rare species grouped together and abundant species grouped together) and accounts for different areas swept by trawls for the site classification. Both species-species and trawl-trawl similarity matrices were clustered using a group average sorting strategy and presented in the form of dendrograms.

Species diversity (H') was calculated from the Shannon-Wiener information function (Shannon and Weaver, 1963; Pielou, 1966). Diversity was also calculated by rarefaction (Sanders, 1968), as modified by Hurlbert (1971), where the expected number of species, $E(S_n)$, is based on drawing at random, without replacement, varying numbers of individuals from a hypergeometric distribution of individuals from a population or, in this case, a trawl. Diversity values are sensitive to species richness and evenness (Lloyd and Ghelardi, 1964). Species richness (SR) was estimated by $SR = (S - 1)/\ln N$ where S is the number of species and N is the number of individuals in a grouping (Margalef, 1958). Evenness (J') was calculated after Pielou (1966) as $J' = H'/\log_2 S$. Values for evenness approach zero when dominance is high and are 1.0 when all species present are represented by an equal number of individuals. Diversity, species richness and evenness values were determined based on both biomass and density of all species. Dominant species were determined by a ranking procedure (Fager, 1957) where the most abundant species in a trawl was given the value of 20, the next 19, and so on. The ranks were summed for each trawl considered and divided by the total number of trawls summed. The resultant biological index includes both frequency of occurrence and abundance in determining dominant species.

Venezuela Basin megafauna were categorized into feeding types, i.e., deposit feeders, suspension feeders, or predators. Categorization was accomplished by investigation of gut contents or inference from feeding organ morphology (Gore, 1983, 1984, 1985a,b; Briggs,

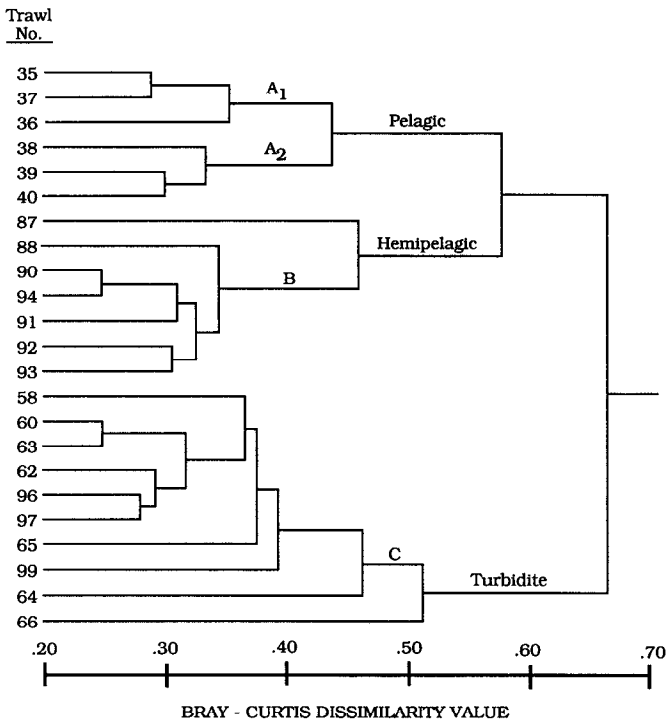


Figure 2. Dendrogram of site groups based on group-average sorting of Bray-Curtis dissimilarity values between all possible pairs of stations (based on abundance data).

1985; Crabtree and Sulak, 1986; Cartes and Abelló, 1992). Omnivorous species invariably consume sediment as a consequence of their feeding behavior, and therefore were grouped with the sediment deposit feeders. Sponges, sea pens, anemones, pectinid bivalves, and stalked barnacles were designated suspension-feeders. Fishes, cephalopods, and most of the gastropods (e.g., the Turridae: P. Mikkelsen, pers. communication) were considered predatory megafauna.

3. Results

Sponges made up a significant volume of the hauls from the Venezuela Basin, especially at the hemipelagic site. Although 11 species of siliceous sponges were identified from the hauls, it was impossible to distinguish individual specimens from the fragmented colonial organisms.

Site groupings based on classification techniques corresponded to the *a priori* division of trawl sites into hemipelagic, pelagic, and turbidite provinces (Fig. 2). Classification groupings based on species density and biomass were nearly identical (Figs. 2 and 3). The separation of trawls collected from the pelagic province into groups A₁ (trawls 35, 36, and 37) and A₂ (trawls 38, 39, and 40) may represent an increased proficiency in trawling as the

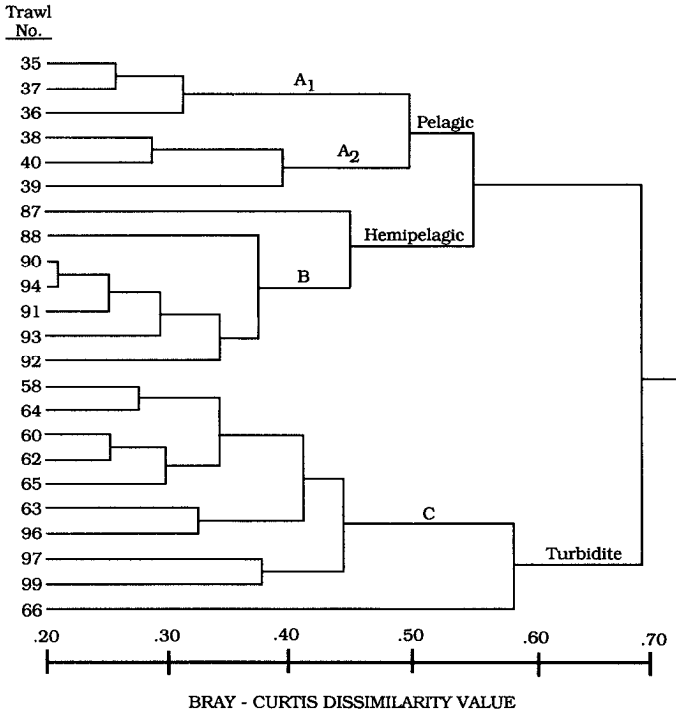


Figure 3. Dendrogram of site groups based on group-average sorting of Bray-Curtis dissimilarity values between all possible pairs of stations (based on biomass data).

crew became more familiar with the equipment. Values of biomass and density of the more motile fishes and decapods as well as the larger holothurians were higher in trawls collected later (group A₂) compared to earlier trawls (group A₁). Trawls collected in the hemipelagic province (trawls 88, 90, 91, 92, 93 & 94) were very similar with respect to the relative distribution of density and biomass among species. The dissimilarity of trawl 87 to other trawls collected in the hemipelagic province reflects the low density and biomass of motile fishes and decapods, suggesting inefficient trawling. Trawls collected in the deepest turbidite province clustered into group C, based on values of both species density and biomass. Trawl 66, based on both density and biomass classifications, was somewhat dissimilar to other trawls collected from the turbidite province. This trawl sampled a small, uncharted rise (120 m in height) in the middle of the turbidite plain collecting an unusually large number of the holothurian *Pseudostichopus atlanticus* (64 specimens, total wt.: 13.4 kg). Based on the correspondence between the results of faunal classification and an *a priori* division of trawl sites based on depth and sediment type, we retained the pelagic, hemipelagic and turbidite trawl groupings for diversity, evenness, and species richness calculations (Table 4).

Classification of species, based on abundance and biomass value distributions among trawls, yielded three major groupings (Figs. 4 and 5). Species group A, consisting of

Table 4. Megafaunal diversity, evenness (J') and species richness (SR) calculated for trawl stations based on species density or biomass. Species diversity based on information theory (H') or on rarefaction ($E[S_n]$). The expected number of species is based on 62 individuals for megafauna density and 228 grams wet weight for megafauna biomass.

Province	Sta.	Density				Biomass			
		H'	$E[S_{62}]$	J'	SR	H'	$E[S_{228}]$	J'	SR
Pelagic	35	3.6	15.6	0.87	2.5	3.0	18.2	0.67	2.4
	36	3.6	18.0	0.86	2.9	2.5	16.0	0.58	2.4
	37	4.0	18.5	0.90	3.1	2.8	17.6	0.60	2.6
	38	4.1	19.8	0.83	4.1	3.6	21.6	0.71	3.2
	39	3.9	19.0	0.72	4.6	3.4	20.2	0.62	3.3
	40	4.1	20.3	0.81	3.8	3.2	17.9	0.62	2.9
Turbidite	58	2.7	11.9	0.76	1.8	0.6	6.8	0.16	1.1
	60	2.8	13.4	0.73	2.1	1.4	9.1	0.34	1.4
	62	2.7	11.7	0.67	2.2	0.9	9.8	0.21	1.5
	63	3.2	14.1	0.75	2.6	1.7	9.2	0.38	1.5
	64	0.9	6.1	0.31	1.0	0.4	6.0	0.11	0.9
	65	3.6	17.2	0.83	2.9	1.1	10.7	0.25	1.8
	66	1.8	8.1	0.46	1.8	0.9	7.6	0.21	1.2
	96	2.1	11.0	0.48	2.6	1.9	12.4	0.41	1.9
	97	2.0	9.1	0.51	1.9	2.9	15.1	0.69	1.7
	99	2.5	12.2	0.61	2.4	3.0	16.0	0.66	1.9
Hemipelagic	87	3.6	17.4	0.82	3.2	2.2	14.1	0.47	2.1
	88	4.1	20.6	0.76	5.0	2.8	18.0	0.51	3.5
	90	4.4	23.3	0.81	5.3	2.4	18.1	0.43	3.5
	91	4.1	21.3	0.76	5.2	2.7	19.6	0.48	3.5
	92	4.3	22.3	0.78	5.4	2.5	16.6	0.44	3.5
	93	4.1	20.4	0.78	4.6	2.3	17.0	0.42	3.0
	94	4.5	24.8	0.84	5.1	2.6	20.6	0.46	3.4

filter-feeding coelentrates (*Umbellula thomsonii* and *Kophobelemnon* sp.), a deposit-feeding sipunculid (*Sipunculus lomonsovi*), and a predatory gastropod (*Pleurotomella lepticoncha*) was restricted to the pelagic province. The deposit-feeding sipunculid *Arhynchite inamoenus* and a filter-feeding barnacle *Scalpellum regium* were also restricted to the pelagic province (Table 5).

Species group B contained many wide-ranging species. Species in subgroup B₁ were found in trawls from all provinces and included a filter-feeding anemone (*Monactis vestita*); deposit-feeding decapods (*Willemoesia indica* and *Plesiopenaeus armatus*), asteroids (*Thoracaster cylindricus* and *Styracaster horridus*), holothurians (*Benthoctes typica* and *Psychropotes semperiana*), and predatory fishes (*Bassozetus* sp. and *Bathyonus laticeps*). Species in subgroup B₂ were primarily found in trawls from the turbidite province and included a filter-feeding barnacle (*Scalpellum flavum*), a deposit-feeding asteroid (*Pteraster acicula*), and deposit-feeding decapods (*Munidopsis crassa* and *Glyphocrangon atlantica*). All but *P. acicula* were also collected in trawls from the pelagic

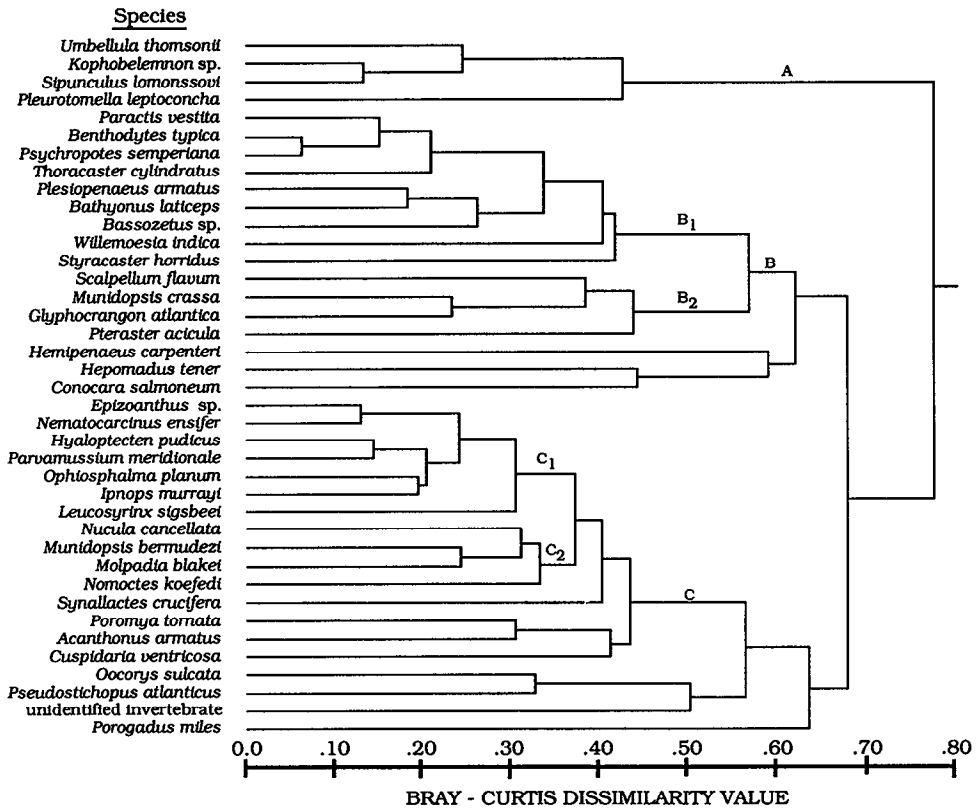


Figure 4. Dendrogram of species groups based on group-average sorting of Bray-Curtis dissimilarity values between all possible pairs of species (based on abundance data).

province. Species in group C were abundant in trawls collected from the shallower pelagic and hemipelagic provinces. Species in subgroup C₁ were primarily restricted to the hemipelagic province and included the filter-feeding anemone *Eptzoanthus* sp., the predatory gastropod *Leucosyrinx sigsbeeii*, filter-feeding bivalves *Hyaloptecten pudicus* and *Parvamussium meridionale*, the deposit-feeding decapod *Nematocarcinus ensifer*, the deposit-feeding ophiuroid *Ophiosphalma planum*, and the predatory fish *Ipnotis murrayi*. The predatory gastropod *Boreotrophon aculeatus*, the deposit-feeding gastropod *Calliotropis infundibulum*, the deposit-feeding scaphopod *Fissidentalium meridionale verrilli* and deposit-feeding decapod *Pontophilus talismani* were also restricted to the hemipelagic province (Table 5). Species common to both pelagic and hemipelagic provinces included the deposit-feeding bivalves *Nucula cancellata*, *Poromya tornata* and *Cuspidaria ventricosa*, the deposit-feeding decapod *Munidopsis bermudezi*, the deposit-feeding holothurians *Molpadia blakei* and *Synallactes crucifera*, and the predatory fishes *Nomoctes koefedi* and *Acanthonus armatus*.

Classification of species by biomass yielded similar results, but included six species of

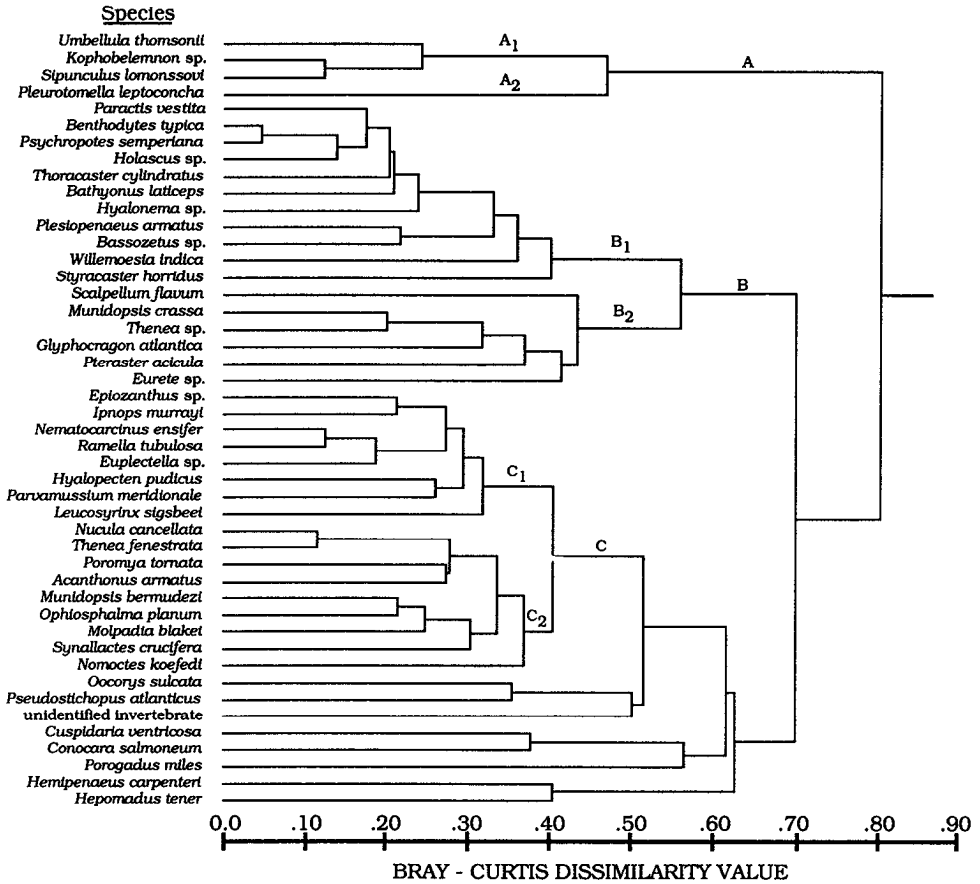


Figure 5. Dendrogram of species groups based on group-average sorting of Bray-Curtis dissimilarity values between all possible pairs of species (based on biomass data).

filter-feeding sponges which were not considered in the analysis of abundance data. *Holascus* sp. and *Hyalonema* sp. clustered with species subgroup B₁, *Thenea* sp. and *Eurette* sp. clustered with subgroup B₂, *Thenea fenestrata* clustered with group C and *Euplectella* sp. clustered with subgroup C₁.

The catch rates, including biomass and density, of major megafaunal taxa are summarized in Table 3. Sponges dominated the biomass of fauna in trawls collected in the turbidite and hemipelagic provinces; whereas, biomass of trawls collected from the pelagic province was dominated by fishes. Coelenterates and holothurians were abundant in trawls collected from all provinces; mollusks, decapods and fishes were most abundant in trawls collected from the pelagic and hemipelagic provinces.

Diversity values determined by rarefaction and information theory were highly correlated whether calculated on the basis of species density ($r^2 = 0.95$) or biomass ($r^2 = 0.85$). Megafaunal diversity (Table 4; Figs. 6 and 7), expressed as H' or $E(S_n)$, was lower in trawls

Table 5. Catch rates of megafauna species in terms of number and biomass wet weight per hour hauled from the three sedimentary provinces in the Venezuela Basin.

Species	Pelagic		Turbidite		Hemipelagic	
	Number	Weight	Number	Weight	Number	Weight
Porifera						
<i>Radiella</i> sp.	—	0.64	0	0	0	0
<i>Thenea fenestrata</i>	—	206.56	0	0	—	1741.45
<i>Thenea</i> sp.	0	0	—	1068.70	0	0
<i>Malacosaccus</i> sp.	0	0	0	0	—	0.22
<i>Caulophacus</i> sp.	0	0	—	0.92	0	0
<i>Hyalonema</i> sp.	—	1.68	—	2.64	—	13.13
<i>Holascus</i> sp.	—	14.24	—	40.30	—	282.74
<i>Myriastr</i> sp.	0	0	0	0	—	1.18
<i>Euplectella</i> sp.	0	0	0	0	—	19.17
<i>Asbestopluma</i> sp.	—	0.05	0	0	0	0
<i>Eurete</i> sp.	—	0.13	—	0.40	0	0
<i>Ramella tubulosa</i>	0	0	0	0	—	6.52
Coelenterata						
<i>Umbellula thomsonii</i>	5.00	1.13	0	0	0.29	0.07
<i>U. lindahl</i>	0.67	0.39	0	0	0	0
<i>Kophobelemnon</i> sp.	2.63	1.54	0	0	0	0
<i>Monactis vestita</i>	6.17	2.53	20.06	7.81	6.36	2.61
<i>Amphianthus</i> sp.	0.32	0.02	0.02	0.02	0.42	0.39
<i>Phelliactis michaelisars</i>	0	0	0	0	0.30	48.27
<i>Epizoanthus</i> sp.	0	0	0.04	0.01	2.39	0.28
Gastropoda						
<i>Calliotropis infundibulum</i>	0	0	0	0	0.39	0.18
<i>Oocorys sulcata</i>	0	0	0.21	0.90	0.23	0.72
<i>Boreotrophon aculeatus</i>	0	0	0	0	0.39	0.09
<i>Beringius brychius</i>	0.45	0.76	0	0	0.07	0.10
<i>Morrisonella</i> sp.	0	0	0	0	0.21	0.08
<i>Ptychosyrinx carynae</i>	0.04	0.01	0	0	0.12	0.10
<i>Leucosyrinx sigsbeeii</i>	0.06	0.03	0.02	0.003	0.49	0.26
<i>Aforia</i> sp.	0	0	0.03	0.27	0	0
<i>Benthomangelia decapitata</i>	0	0	0	0	0.17	0.02
<i>Pleurotomella leptoco</i>	0.42	0.92	0.07	0.41	0	0
<i>P. chariessa</i> var. 1	0.12	0.05	0	0	0	0
<i>P. chariessa</i> var. 2	0.11	0.01	0	0	0.11	0.31
<i>P. eurybrocha</i>	0.09	0.02	0	0	0	0
<i>P. parkardii benedicti</i>	0	0	0	0	0.05	0.03
<i>P. bruneri</i>	0.10	0.04	0	0	0	0
<i>Gymnobela frielei</i>	0.06	0.05	0.02	0.06	0	0
<i>G. engonia</i>	0	0	0	0	0.04	0.01
Pelecypoda						
<i>Nucula cancellata</i>	3.86	1.59	0	0	4.70	2.39
<i>Hyalopecten pudicus</i>	0	0	0	0	0.67	0.33
<i>Parvamussium meridionale</i>	0	0	0	0	1.13	0.19

Table 5. (Continued)

Species	Pelagic		Turbidite		Hemipelagic	
	Number	Weight	Number	Weight	Number	Weight
<i>Limatula confusa</i>	0	0	0.02	0.002	0	0
<i>Abra longicallis americana</i>	0	0	0	0	0.03	0.02
<i>Abra nov. sp.</i>	0	0	0	0	0.07	0.01
<i>Poromya tornata</i>	2.48	0.97	0	0	0.77	0.49
<i>Verticordia triangularis</i>	0	0	0	0	0.17	0.07
<i>Lyonsiella smidti</i>	0.39	0.15	0	0	0	0
<i>Cuspidaria turgida</i>	0	0	0	0	0.03	0.004
<i>C. ventricosa</i>	0.11	0.16	0	0	0.20	0.82
<i>C. abyssicola</i>	0	0	0	0	0.05	0.12
<i>C. notabilis</i>	0	0	0	0	0.18	0.15
Scaphopoda						
<i>Fissidentalium meridionale</i> <i>verrilli</i>	0	0	0	0	3.97	4.04
Cephalopoda						
<i>Grimptoteuthis sp.</i>	0.28	1.43	0.04	0.17	0	0
<i>Opisthoteuthis agassizi</i>	0	0	0	0	0.04	2.11
<i>Stauroteuthis sp.</i>	0.10	0.39	0.02	0.71	0.04	1.61
Cirripedia						
<i>Scalpellum regium</i>	0.57	0.98	0	0	0	0
<i>S. flavum</i>	1.45	0.35	0.69	0.14	0	0
Decapoda						
<i>Munidopsis aries</i>	0.23	16.27	0	0	0.03	2.74
<i>M. bermudezi</i>	0.34	2.72	0	0	1.68	12.45
<i>M. crassa</i>	0.28	0.71	0.75	8.63	0	0
<i>M. geyeri</i>	0	0	0	0	0.08	0.51
<i>Willemoesia indica</i>	2.30	23.55	0.29	9.36	1.12	29.00
<i>W. forceps</i>	0.06	0.32	0	0	0.31	9.98
<i>Willemoesia sp.</i>	0	0	0.04	0.04	0	0
<i>Ethusina abyssicola</i>	0.24	0.42	0.07	0.14	0.05	0.09
<i>Glyphocrangon atlantica</i>	0.76	2.38	0.74	2.88	0	0
<i>Nematocarcinus ensifer</i>	0	0	0	0	0.74	1.38
<i>Pontophilus talismani</i>	0	0	0	0	0.24	0.16
<i>Plesiopenaeus armatus</i>	1.30	38.85	0.15	3.18	0.95	25.19
<i>Benthesicymus iridescens</i>	0.06	0.19	0.02	0.06	0.13	0.19
<i>Hemipenaeus carpenteri</i>	0.21	0.93	0.07	0.54	0.20	1.65
<i>H. tridens</i>	0	0	0	0	0.04	0.79
<i>Hepomadus tener</i>	0.15	2.51	0.10	0.58	0.21	2.87
Sipuncula						
<i>Sipunculus lomonssovi</i>	5.20	12.59	0	0	0.04	0.01
<i>Nephasoma improvisa</i>	0	0	0	0	0.08	0.03
<i>Arhynchite inamoenus</i>	1.7	0.95	0	0	0	0
Echiura						
<i>Kurchatovus epeudentatus</i>	0	0	0.02	<0.001	0.09	0.01

Table 5. (Continued)

Species	Pelagic		Turbidite		Hemipelagic	
	Number	Weight	Number	Weight	Number	Weight
<i>Bonellia suhmii</i>	0	0	0.03	0.03	0	0
unidentified echiuria	0	0	0.06	0.01	0	0
Asteroidea						
<i>Thoracaster cylindratus</i>	4.36	37.89	0.72	12.25	2.66	63.13
<i>Styracaster horridus</i>	1.50	13.62	0.44	3.85	0.34	5.72
<i>Caymanostella spinimarginata</i>	0.98	0.03	0.02	0.001	0.12	0.01
<i>Pteraster acicula</i>	0	0	0.54	2.03	0.09	0.37
Echinoidea						
<i>Sarsiaster griegii</i>	0	0	0	0	0.05	0.15
unidentified spatangoid	0	0	0.02	0.01	0.03	0.03
Ophiuroidea						
<i>Silax verrilli</i>	0	0	0.96	0.01	0	0
<i>Ophiosphalma planum</i>	0.13	0.12	0	0	3.42	2.36
<i>Perlophiura profundissima</i>	0	0	0	0	0.03	<0.001
Holothuroidea						
<i>Benthoctes typica</i>	7.18	20.73	3.18	11.15	11.48	35.47
<i>Benthoctes lingua</i>	0	0	0	0	0.17	74.48
<i>Psychropotes semperiana</i>	5.61	58.20	3.34	48.61	9.50	185.04
<i>Molpadia blakei</i>	0.33	0.59	0.04	0.14	1.46	3.29
<i>Synallactes crucifera</i>	0.18	0.62	0.12	0.65	0.70	2.49
<i>Pseudostichopus atlanticus</i>	0.10	0.15	1.96	409.83	0.93	87.24
<i>Ps. sp.</i>	0.06	20.40	0	0	0.08	34.12
<i>Paroriza prouhoi</i>	0.10	0.21	0	0	0	0
unidentified invertebrate	0.40	0.87	0.02	0.02	0.46	1.34
Pisces						
<i>Haptenchelys texis</i>	0.11	3.67	0	0	0	0
<i>Bathytroctes microlepis</i>	0.06	4.02	0	0	0	0
<i>Conocara salmoneum</i>	0.11	44.17	0.06	4.48	0.12	125.36
<i>Nomoctes koefedi</i>	0.16	1.60	0	0	0.52	51.69
<i>N. michaelsarsi</i>	0	0	0.02	2.84	0	0
<i>Rinoctes nasutus</i>	0	0	0	0	0.37	5.37
juvenile Alepocephalidae	0	0	0.04	0.79	0.05	0.38
<i>Bathypterois grallator</i>	0.35	30.09	0	0	0	0
<i>Bathytrophops sewelli</i>	0	0	0	0	0.04	3.14
<i>Ipnops murrayi</i>	0	0	0	0	0.61	3.29
<i>Bathysaurus mollis</i>	0.11	132.44	0.03	2.18	0.10	69.53
<i>Thaumatichthys binghami</i>	0.06	0.11	0	0	0.04	0.20
<i>Aphyonus rassi</i>	0	0	0.02	0.06	0	0
<i>A. sp.</i>	0	0	0.06	0.19	0	0
<i>Nybelinella eriksseni</i>	0	0	0.04	0.11	0	0
<i>Acanthonus armatus</i>	1.05	40.48	0	0	1.50	46.38
<i>Apagasoma edentatum</i>	0	0	0.04	144.48	0	0
<i>Barathrites iris</i>	0	0	0.04	64.84	0	0
<i>Bassozetus sp.</i>	0.94	216.55	0.71	51.43	0.46	120.58

Table 5. (Continued)

Species	Pelagic		Turbidite		Hemipelagic	
	Number	Weight	Number	Weight	Number	Weight
<i>Bathyonus laticeps</i>	15.42	108.70	0.72	10.55	3.33	29.50
<i>Holcomycteronus squamosus</i>	0.06	4.22	0.02	0.25	0.05	4.00
<i>Penopus macdonaldi</i>	0	0	0	0	0.17	0.87
<i>Porogadus catena</i>	0	0	0	0	0.04	0.52
<i>P. miles</i>	0	0	0.07	0.80	0.15	7.28
<i>Coryphaenoides macrocephalus</i>	0	0	0	0	0.05	6.08
<i>Pachycara nov. sp.</i>	0	0	0	0	0.03	0.47

from the turbidite site than from trawls from the shallower pelagic and hemipelagic sites (Mann-Whitney U -test, $p < 0.001$ level of significance). Both lower species richness (SR) and lower evenness (J') contribute to the lower values of diversity.

Catch rates for the 121 species of megafauna were calculated in terms of number and biomass and are presented for the three sedimentary provinces in Table 5. Of the 23 species collected in common among the three provinces, only 10 were ranked as dominant species. Species which ranked dominant within each province were generally species commonly found throughout the Venezuela Basin (i.e., species group B_1), and not those restricted to

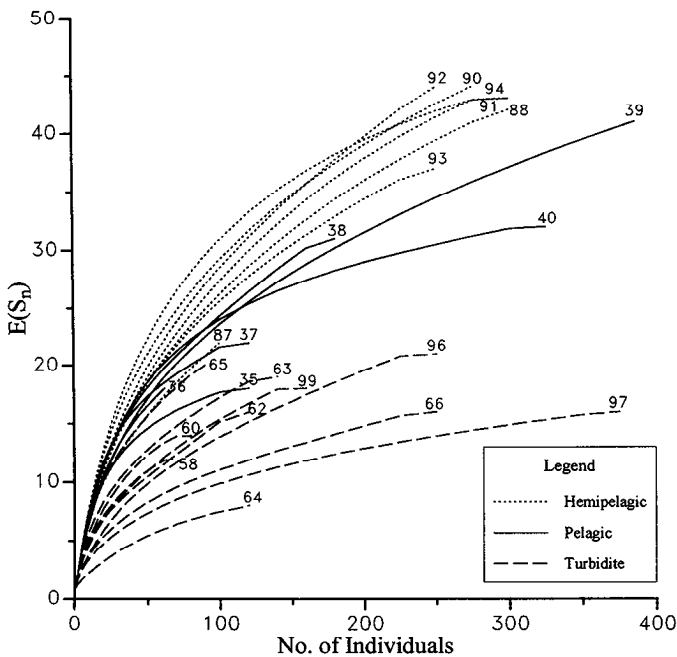


Figure 6. Rarefaction curves of expected species diversity based on megafauna density in each of the 23 trawls collected from the Venezuela Basin.

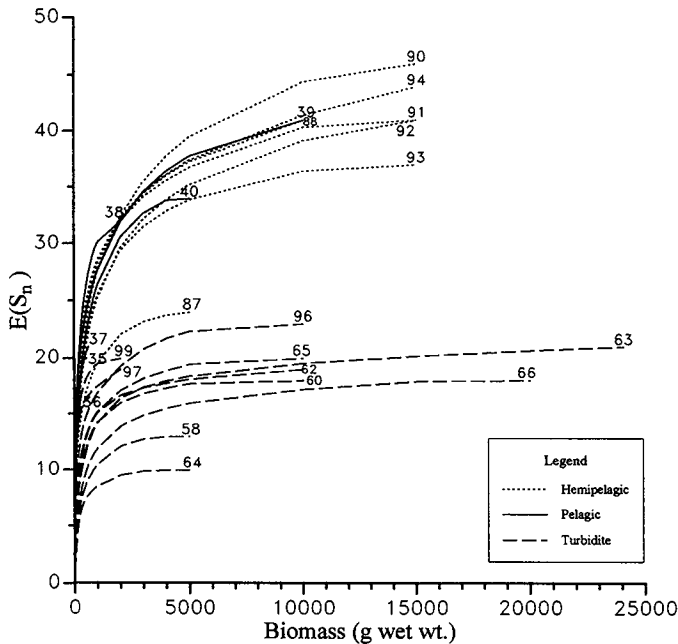


Figure 7. Rarefaction curves of expected species diversity based on megafauna biomass in each of the 23 trawls collected from the Venezuela Basin.

one or two provinces. The species comprising species group B₁ were the stalked sponge *Hyalonema* sp. and the euplectellid sponge *Holascus* sp., the anemone *Monactis vestita*, the abyssal lobster *Willemoesia indica*, the asteroids *Thoracaster cylindratus* and *Styracaster horridus*, the holothurians *Bentho-dytes typica* and *Psychropotes semperiana*, and the fishes *Bassozetus* sp. and *Bathyonus laticeps*. The importance of the anemone *Monactis vestita* was probably amplified by the abundance of available substrate on which the polyps lived. Its relatively high catch rate of 20.06 individuals h⁻¹ at the turbidite province was related to the abundance of coal, coal clinker, and tar balls jettisoned from vessels transiting a major shipping route above the abyssal plain. Similarly, the siliceous stalks of sponges like *Hyalonema* provided a substrate on which the anemone *Amphianthus* sp. and the brachiopods grew.

The psychropotid holothurians *Bentho-dytes typica* and *Psychropotes semperiana* and the sipunculan worm *Sipunculus lomonosovi* were members of the pelagic province. Examination of the sediment from their guts revealed these species to be surface deposit feeders (Briggs, 1985). The dominant species by wet weight at the pelagic province were the sponge *Thenia fenestrata*, the holothurian *P. semperiana*, and the porcellanasterid sea star *Thoracaster cylindratus*. The higher abundance of the filter-feeding sponge could imply its dominance in terms of numbers as well as biomass. Analysis of gut contents revealed that the sea star and holothurians were *de facto* selective deposit feeders, ingesting exclusively the upper 5 mm of sediment (Briggs, 1985). The numerically dominant species

collected by trawls from the turbidite province were the hormathiid anemone *Monactis vestita* and the holothurians *P. semperiana* and *B. typica*. These two holothurians were dominant also in terms of biomass, but the sponge *Thenea* sp. was ranked the highest in all trawls from the turbidite province. The numerically dominant species at the hemipelagic province were *B. typica*, *P. semperiana*, and *M. vestita*. The sponges *T. fenestrata* and *Holascus* sp. and the holothurian *P. semperiana* were dominant in terms of biomass hauled from the hemipelagic province.

4. Discussion

a. Comparisons with selected deep-sea megafaunal studies. Megafaunal data from this study are in agreement with the general decrease in megafaunal density and biomass with distance from land and the predominance of filter-feeding, siliceous sponges reported from the AKADEMIK KURCHATOV expedition to the Caribbean Sea (Kuznetsov *et al.*, 1974; Pasternak *et al.*, 1975).

For direct comparisons of abundance and biomass, only Haedrich *et al.* (1975, 1980) and Thurston *et al.* (1994) provide complete megafaunal data sets using comparable net and mesh sizes. Values of megafaunal biomass and density from the Venezuela Basin appear to be close to the lower end of values reported in these studies from abyssal sites in the Atlantic. Although values of megafauna biomass are commensurate, values of megafauna density in the Venezuela Basin are 12 to 50% of the megafauna density south of New England (Haedrich *et al.*, 1980). Values of megafauna density in the Venezuela Basin are 19 to 42% of the megafauna density in the Porcupine abyssal plain (Thurston *et al.*, 1994). The Venezuela Basin and the Madeira abyssal plain exhibit similar densities of megafauna (Thurston *et al.*, 1994). Values of megafauna biomass from the Venezuela Basin (48.6–143.6 g 10³ m⁻²) slightly exceed the megafauna biomass found by Thurston *et al.* (1994) for the Madeira abyssal plain (35.82 g 10³ m⁻²), but fall short of the megafauna biomass (392.3 g 10³ m⁻²) found by the same authors for the Porcupine abyssal plain. The disparity between values of Venezuela Basin and Porcupine abyssal plain megafauna biomass is even greater when the biomass of sponges is ignored.

A comparison of average surface productivity from the various basins (derived from Berger, 1989) with megafauna densities conforms in the most general manner to the positive trend presented by Thurston *et al.* (1994, p. 1342). Differences in megafauna biomass within sites in the Atlantic, specifically between the Porcupine and Madeira abyssal plains, are attributed by Thurston *et al.* (1994) to the seasonal arrival of phytodetritus on the Porcupine abyssal plain sea floor. Differences in megafauna biomass within sites in the Venezuela Basin are probably likewise related to differences in the nature of the particulate flux to the sea floor. Low particulate flux is characteristic of the pelagic site in the Venezuela Basin and the Madeira abyssal plain but slow, pelagic sedimentation is overwhelmed by terrestrial sedimentation at the turbidite and hemipelagic sites. Hence, factors controlling the density and biomass of megafauna in the deep sea appear to be related to site-specific biological and environmental interactions.

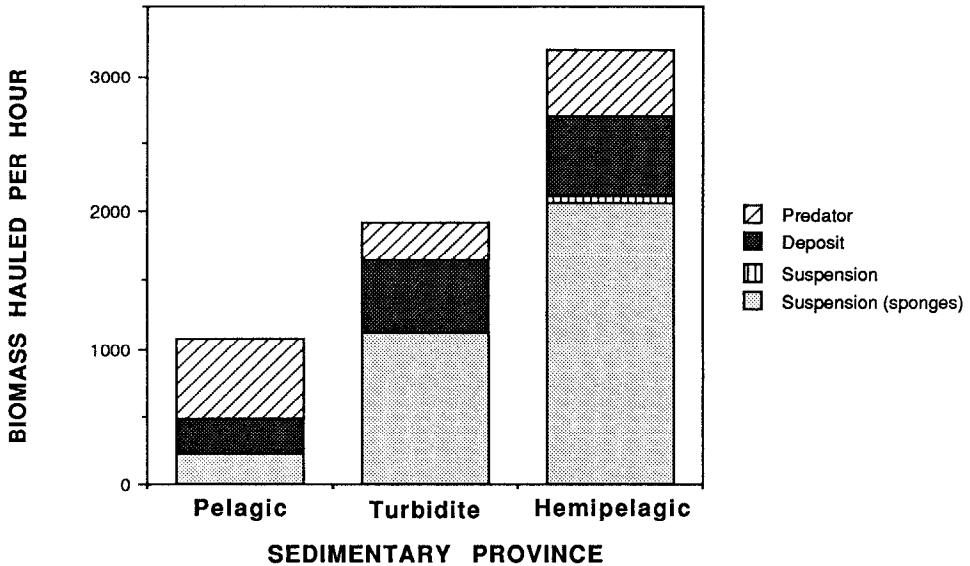


Figure 8. Biomass of feeding types based on catch rates in wet weight (g) hauled h^{-1} from the three sedimentary provinces in the Venezuela Basin.

b. Biological and environmental interactions in the Venezuela Basin. Faunal assemblages were classified into site groupings which correspond to the *a priori* division of trawl sites into three provinces (pelagic, hemipelagic and turbidite). This correspondence suggests that megafaunal assemblages respond to common environmental factors within each province associated with depth, sediment type, or food resources. Venezuela Basin megafauna were categorized as deposit feeders, suspension feeders, or predators (Figs. 8 and 9). Most species were deposit feeders: echinoderms, sipunculans, echiurans, most decapods, most bivalves, and some gastropods. Deposit feeders attained the greatest biomass at the turbidite and hemipelagic provinces. Total abundance of deposit feeders, however, was greatest at the pelagic and hemipelagic provinces. Although abundance of predators is lowest at the turbidite province, biomass of individual predators is high, resulting in fewer, but larger carnivores in the deepest part of the basin. As a consequence of the overwhelming contribution of the sponge biomass, suspension feeders dominated hemipelagic and turbidite provinces. The predominance of sponges and the larger size of predators from deeper parts of the Venezuela Basin were also observed by Pasternak *et al.* (1975) in early studies.

Decreases in bottom water temperature and increases in pressure associated with depth are unlikely to account for distribution of megafauna in the Venezuela Basin. Bottom water temperature is nearly uniform below 2300 m in the basin and the hydrostatic pressure increase between 3500 m and 5050 m water depth is not likely to affect enzymatic adaptations to pressure which occur at 500 and 3000 m (Somero, 1990). We, therefore, suggest that environmental factors associated with sediment type, biological interactions,

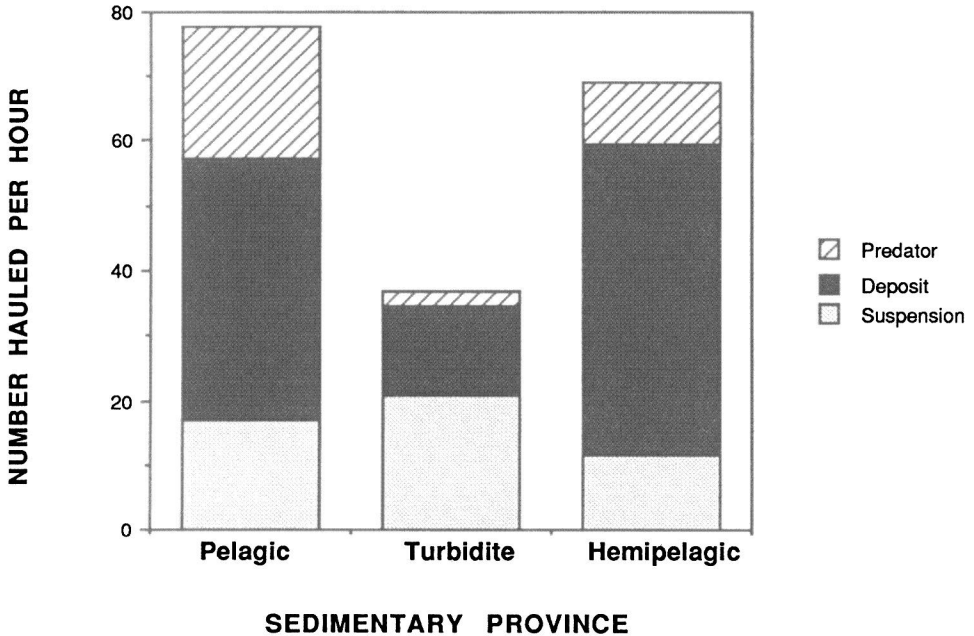


Figure 9. Abundance of feeding types based on catch rates in number of individuals hauled h^{-1} from the three sedimentary provinces in the Venezuela Basin.

disturbance, or trophic factors such as food types and/or availability probably account for the distribution of megafaunal assemblages.

Substrate selection by sessile organisms may affect community structure by virtue of the presence of anthropogenic debris. Coal clinker present at the turbidite province provide hard substrate for the colonization by the suspension feeding anemone *Monactis vestita*. Kidd and Huggett (1981) discovered that clinker is the most abundant debris material beneath shipping lanes in the North Atlantic. In the turbidite province, *Monactis vestita* accounts for 57% of the megafaunal density but less than 1% of the faunal biomass. The potential trophic role of epifauna in deep-sea benthic communities where hard substrata are available has been noted by Mullineaux (1987) in the North Pacific and Hecker (1990) and Christiansen and Thiel (1992) in the North Atlantic.

Sponges typically constitute a minor portion of the megafaunal community and have a lower organic content than other taxa (Haedrich *et al.*, 1980; Rowe, 1983; Thurston *et al.*, 1994). Their large biomass relative to the other taxa and their peculiar abundance patterns in relation to the three sites, however, warrant their discussion as a biological interaction. Sponges provide important habitat for attached organisms and allow commensal relationships to develop. The role of sponges as a structural component rather than a direct trophic link within benthic communities has been suggested previously for Antarctic species by Barthel (1995). Anemones and brachiopods attached to sponges were recovered from the Venezuela Basin stations and the bivalves *H. pudicus* and *P. meridionale* showed evidence

of byssal attachment. Lampitt *et al.* (1986) also reported a collection of fauna which are commensal with the sponge *Thenea*, a common species in the Venezuela Basin (Table 5).

Flux of particulate organic matter would be expected to be high at the hemipelagic province which is the shallowest, the greatest recipient of fine terrigenous material, and in the area of highest water column productivity in the Venezuela Basin (Bowles and Fleischer, 1985; Couper, 1983). Loss of eddy kinetic energy of currents flowing over the Aves Ridge along with other hydrodynamic influences are postulated by Kinder *et al.* (1985) to cause a rapid diminution of flux of suspended material to the sea floor as the predominant water transport moves from east to west across the basin. The physical characteristics of sediments reflect this deposition pattern with progressively less terrigenous material from the hemipelagic, to turbidite and pelagic provinces (Briggs *et al.*, 1985). This material is organically rich (Shaw and Johns, 1985), offers a sorptive site for dissolved organic matter and substrate for bacteria (Baird and White, 1985), and provides an important source of food for benthic animals. Biomass of the predominant deposit- and suspension-feeding macro- and megafauna reflected this presumed east-to-west decrease in flux of particulate organic matter to the sea floor of the Venezuela Basin (Richardson and Young, 1987).

There is not, however, a strict interdependence of abundance or biomass of megafauna and the amount of sediment organic matter in the three sedimentary provinces. Sediment organic carbon and nitrogen content is highest at the turbidite province, yet the hemipelagic province displays the largest biomass in all size classes of benthos (Richardson and Young, 1987). The coincidence of higher values of biomass in the turbidite and hemipelagic provinces and higher amounts of sediment organic nitrogen in these eastern provinces as compared with the pelagic province could be indicative of the effect of qualitative differences in organic matter on secondary production (Tenore and Rice, 1980). Yet, carbon:nitrogen ratios of the sediment organic matter, the only measurement we have from which food quality may be inferred, are essentially equivalent among the three provinces (approx. 5.4). Moreover, if calcium carbonate is excluded from the sediment weight, approximately the same percentage of organic matter is associated with non-carbonate detrital clays at every province. Hence, detrital carbonate in the form of foraminiferan tests and coccoliths may simply dilute the organic matter available for deposit feeders. The lack of a positive relationship between sediment organic matter and megafaunal standing stock is not surprising. Tietjen *et al.* (1989) have demonstrated that flux of organic carbon to the sea floor is a better indicator of deep-sea faunal biomass than sediment organic carbon concentration.

If decreasing food concentration is structuring the benthic community, then smaller organisms may dominate food-limited assemblages (Thiel, 1975). Overall size of megafauna, expressed as wet weight per individual hauled per hour, does decrease accordingly with decreasing sediment organic matter, but this relationship does not hold true for all taxa (see Polloni *et al.*, 1979, for other examples). Individual species of suspension feeders (exclusive of sponges) in the hemipelagic province and individual species of predators in

the turbidite province are an order of magnitude larger than the same groups in the other two provinces (Table 5). There are no significant differences, however, in the average sizes of deposit-feeding species at the three provinces.

X-radiographs of cores indicate the presence of death assemblages beneath the most recent turbidites deposited in the turbidite province (Briggs *et al.*, 1985). Periodic destruction of the faunal community by catastrophic turbidity flows may control the faunal assemblage at the turbidite province. In this way, disturbance may explain the low abundance of fauna in relation to the organic matter available to consumers. Despite high values of organic carbon and nitrogen in the surface sediment, abundances of megabenthic deposit feeders or their predators are not greater in the turbidite province than at the hemipelagic province (Figs. 8 and 9). Abundance of suspension feeders, however, are greatest at the turbidite province indicating that factors other than disturbance control their abundance.

c. Megafauna diversity. In spite of the numerous studies of deep-sea megafauna, very little data are available on deep-sea megafauna diversity. Haedrich *et al.* (1980) provide the only study where species identifications are sufficient to base diversity comparisons with data from the Venezuela Basin. Rex (1983) calculated Hurlbert's expected number of species for both invertebrate and fish megafauna from the data of Haedrich *et al.* (1975; 1980). Both invertebrate and fish diversity in the NW Atlantic were highest at mid-slope depths and lower at abyssal and shelf depths. This "parabolic" distribution of diversity to depth is in agreement with patterns of diversity of macrofauna groups reported by Rex (1981), but is by no means universal (Gage and Tyler, 1991: pp. 208–209). Diversity of Venezuela megafauna decreased with depth but was considerably higher than calculated by Rex (1983) at equivalent depths (Table 4; Figs. 6 and 7). Reasons for lower species diversity (H' and $E[S_n]$) at the deeper turbidite site, although speculative at best, are lower species richness (SR) as a result of disturbance by repetitive turbidite flows and lower evenness (J') as a result of the high density of the attached filter-feeding coelenterate (*Monactis vestita*), the high collective biomass of the filter-feeding sponge (*Thenea* sp.) and the large contribution to total biomass of a few large, carnivorous fish (*Apagasoma edentatum* and *Barathrites iris*).

d. Zoogeographic distribution of megafauna. The fauna hauled from the Venezuela Basin was typical of the abyssal fauna from the North Atlantic in terms of taxonomic composition (Sibuet *et al.*, 1984; Lampitt *et al.*, 1986; Thurston *et al.*, 1994). Indeed, some of the megafauna species from the Venezuela Basin are panocenic or at least circumtropical in distribution. The stalked barnacle *Scalpellum regium*, for instance is reported to be dredged from the North Atlantic off New England and France, the Indian Ocean, and the Pacific off Australia, New Zealand, and Japan (Zevina, 1970). The pennatulaceans *Umbellula thomsonii* and *U. lindahlii*, however, are endemic only to the Pacific, Indian, and Antarctic Oceans in addition to the Caribbean (Kuznetzov *et al.*, 1974). Among the mollusks, only *A.*

venezuelensis and *L. bartletti*, both newly described species, are known exclusively from the basin. The gastropod *Leucosyrinx sigsbeeii* and the bivalve *Limatula confusa* are native to deep waters off Florida and in the Caribbean. The other gastropods and bivalves, the scaphopod *Fissidentalium meridionale* and the cephalopods, however, are typical western Atlantic mollusks (Abbott, 1974). The polychelid lobster *Willemoesia indica* and the echiuran worm *Kurchatovus epeudentatus* were originally known from specimens collected from the Indian Ocean and Gulf of Aden, respectively (Gore, 1984; A. DattaGupta, pers. communication). It is not certain whether such a disjunct distribution is representative of two zoogeographic distributions or of a paucity of specimens available to taxonomists. The occurrence of some species found in the Venezuela Basin in shallower depths elsewhere (e.g., *K. epeudentatus*, the anemone *Phelliactis michaelsarsi*) may indicate a preference or adaptation of these species for the "warmer" conditions characteristic of the Caribbean basin bottom water (Riemann-Zürneck, 1986). Moreover, the demersal fish *Haptenchelys texis*, *Nomoctes koefoedi*, and *Rinoctes nasutus* are also known from the shallow, warmer waters of the Gulf of Mexico. In general, though, the abyssal fish fauna of the Venezuela Basin is typical of that of the tropical Atlantic (Anderson *et al.*, 1985).

5. Conclusions

A diverse assortment of megafauna (121 species) was collected, enumerated and weighed from 23 benthic trawls from three sedimentary provinces in the Venezuela Basin, ranging in water depth from 3411 to 5062 meters. Only 23 species were collected in common among the three provinces, and of these, only 10 were dominant species.

Separations of taxonomic assemblages in terms of numbers and biomass, among megafauna from the three provinces coincided with distinctions of sedimentary characteristics among the pelagic, hemipelagic and turbidite provinces. Echinoderms were the numerically dominant major megafaunal taxon at the pelagic and hemipelagic provinces, whereas coelenterates were numerically dominant at the turbidite province. Sponges dominated the biomass of megafauna at the hemipelagic and turbidite provinces, whereas fishes dominated at the pelagic province.

Sponges are an important component of the deep-sea community in the Venezuela Basin in that they provide a niche for other epifauna and foster commensal relationships. Because of the difficulties in obtaining unfragmented specimens and the colonial aspect of their morphology, sponges are often overlooked in studies of deep-sea communities.

Jettisoned debris accumulating on the sea floor under major shipping routes provide suitable substrate for attached filter-feeding anemones. The creation of a niche for large numbers of anemones accentuated the importance of suspension feeders and contributed to low diversity values at the turbidite site.

Biomass and abundance of megafauna from the Venezuela Basin are generally less than those of megafauna collected by comparable means at Atlantic abyssal sites. Biomass and average size of megafaunal deposit feeders decrease with the diminution of organic matter

in the sediments. Megafaunal diversity decreases with increasing water depth, but because of concomitant variations in depth, disturbance, sediment type and food resources it is impossible to ascribe the phenomenon to a particular factor. The proximity of sources of organic matter is probably the most important factor responsible for the distribution and composition of *filter-feeding* megafaunal biomass in the Venezuela Basin.

The distribution of biomass in the Venezuela Basin may be explained by proximity to sources of organic matter more than any other factor. The lack of a correlation between sediment organic concentration and megafaunal biomass could be due to the rapid utilization rate of organic matter at the sediment-water interface which results in a nearly identical percentage of refractory organic matter associated with the fine fraction (silt or clay) of sediment in each province. Overall differences in percent organic matter among provinces reflect dilution of the fine fraction by larger particles of calcium carbonate. The resultant lower overall percent organic matter in sediments may affect the biomass and size of deposit feeders. This explanation will remain speculation until more is known of the flux to and quality of organic matter in the sediments of the Venezuela Basin.

The species of megafauna from the Venezuela Basin represent the abyssal megafauna community of the North Atlantic. Several taxonomic groups including the fishes are characteristic of tropical basins and other species may indicate an adaptation for the warmer bottom water of the Caribbean Sea.

Acknowledgments. The manuscript benefited from the suggestions and comments of G. Rowe and E. Gallagher and four anonymous reviewers. The authors thank the following colleagues for taxonomic identification of the trawl catches: J. Miller, P. Mikkelsen, M. Anderson, R. Crabtree, R. Gore, J. Allen, F. Bayer, G. Cooper, E. Cutler, A. DattaGupta, J. DePalma, H. DuShane, W. Emerson, A. Ferreira, M. Harasewych, J. McLean, C. Markle, C. Messing, J. Quinn, M. Rice, K. Riemann-Zürneck, C. R. Robins, K. Ruetzler, J. Ryland, D. K. Serafy, D. Tippett, R. Turner, P. Tyler, N. Voss, T. Waller, and A. Warén. We are indebted to the scientific and ship's crews on the USNS *Bartlett*, cruise 1301-82, for their assistance. This work was supported by program element 61153N, Herbert Eppert, Program Manager. Contribution NRL/JA/7431—93-0010 from the Naval Research Laboratory.

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